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Bennetticarpus yezoites sp. nov. (Bennettitales) from the Upper Cretaceous of Hokkaido, Japan

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Abstract. Recently many plant taxa have been described from the marine Upper Yezo Group (Coniacian-Santonian). These plant fossils are preserved as permineralized debris in calcareous nodules together with various marine animals. A single bennettitalean specimen was collected from the Upper Yezo Group. It consists of a receptacle, with numerous fertile (seminiferous) and sterile (interseminal) scales. Although the specimen is fragmented, its anatomical features are well preserved. This paper provides a description of a new reproductive organ belonging to Bennettitales. As its affinity to Williamsoniaceae or Cycadeoidaceae and their allies is uncertain, we provisionally place our specimen in the form-genus *Bennetticarpus* and describe *B. yezoites* sp. nov. Comparison of *Bennetticarpus yezoites* with known bennettitalean taxa in other regions is given briefly.

Key words: *Bennetticarpus*, Bennettitales, Hokkaido (Japan), Late Cretaceous, Upper Yezo Group.

Introduction

Since the classical study on the Late Cretaceous permineralized plants from Hokkaido, Japan, by Stopes and Fujii (1910), many papers have been published on the fossil plants collected from the Upper Yezo Group (Coniacian-Santonian) of marine origin. The Upper Yezo Group yields abundant fossil plants, and anatomically studied bennettitaleans are not rare, including, for example, *Cycadeoidea petiolata* Ogura (Ogura, 1930), *Cycadeoidella japonica* Ogura (Ogura, 1930 ; Nishida, H., 1991), *Otozamites kerae* Ohana and Kimura (Ohana and Kimura, 1991), *O. takahashii* Ohana and Kimura (Ohana and Kimura, 1991).

Many other taxa known by early 1991 were listed by H. Nishida (1991, p. 256-261). Recently several permineralized conifer taxa were described (e.g., Ohana and Kimura, 1993, 1995 ; Ohsawa *et al*., 1991, 1992, 1992, 1993, 1995 ; Nishida, H. *et al*. 1991 ; Nishida, M. *et al*., 1991, 1992 ; Saiki, 1992 ; Saiki and Kimura, 1993 ; Stockey *et al*., 1993, 1994).

Recently a bennettitalean reproductive organ collected by Yasuji Kera from the Upper Yezo Group in the Yubari area, Hokkaido, Japan, was given to us for the present investigation.

Although the specimen is fragmentary, its unique anatomical structure is well preserved.

It differs from other known bennettitalean taxa, so we place it in the form-genus *Bennetticarpus* following Harris (1932, 1969).

Description

Order Bennettitales
Form-genus ***Bennetticarpus*** Harris, 1932

This form-genus was established by Harris (1932) based on material derived from the Upper Triassic and Lower Jurassic plant-sites in Scoresby Sound, East Greenland. Some authors have used the name of gynoecium or gynoecia for bennettitalean seminiferous scales or both seminiferous and interseminal scales (e.g. Harris, 1932). This form-genus was designated for "all gynoecia which show definitely bennettitalean characters, but which are not fully enough known either to be included in or definitely separated from the existing genera" (Harris, 1932).

Subsequently *Bennetticarpus* has been used by Hsü (1948), Kräusel (1949), Harris (1969) and Watson and Sincock (1992).

Bennetticarpus yezoites sp. nov.

Figures 1-6

Material.—INH-005 (Holotype). Collected by Yasuji Kera. Stored in the Institute of Natural History, Tokyo.

Locality and horizon.—Kaneobetsu Valley (roughly 142°33′02″E, 42°28′52″N), a branch of the Hakkinzawa Valley, Kashima, Yubari City, Hokkaido, Japan (reference map was shown in Ohana and Kimura, 1993 ; figure 1B). Upper Yezo Group of marine origin (Coniacian-Santonian).

Etymology.—Named after Yezo, older name of Hokkaido.

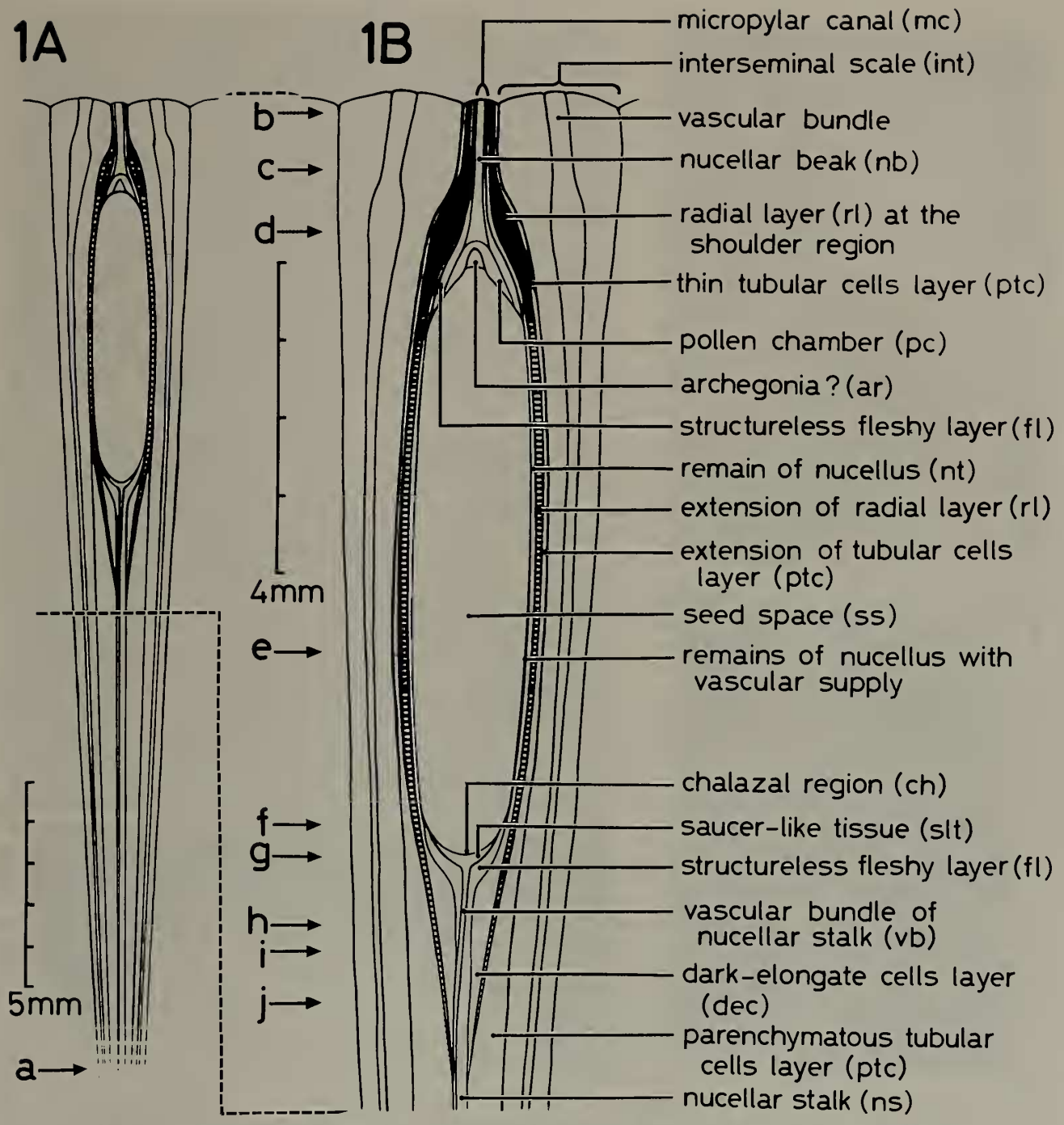

Figure 1. *Bennetticarpus yezoites* sp. nov., **1A**: Radial longitudinal section, showing the whole structure of seminiferous and interseminal scales, except for their basal disintegrated parts (at level a in Figure 1A). **1B**: Distal half of radial longitudinal section of scales, enlarged from Figure 1A. The terminology of tissues is shown on the right side with their abbreviations. Main transversely cut planes are indicated on the left side.

Specific diagnosis.—Large-sized bennettitalean female reproductive organ ('gynoecium'), consisting of a semispherical receptacle covered by densely spaced seminiferous (fertile) and interseminal (sterile) scales, both about 25 mm long.

Seminiferous scale consisting of an orthotropous ovule born on a long, slender stalk with a median bundle consisting of scalariform tracheids. Stalk expanding to saucer-like structure, at the basal part of the seed-space, where vascular bundle diverging laterally and entering the thin nucellus

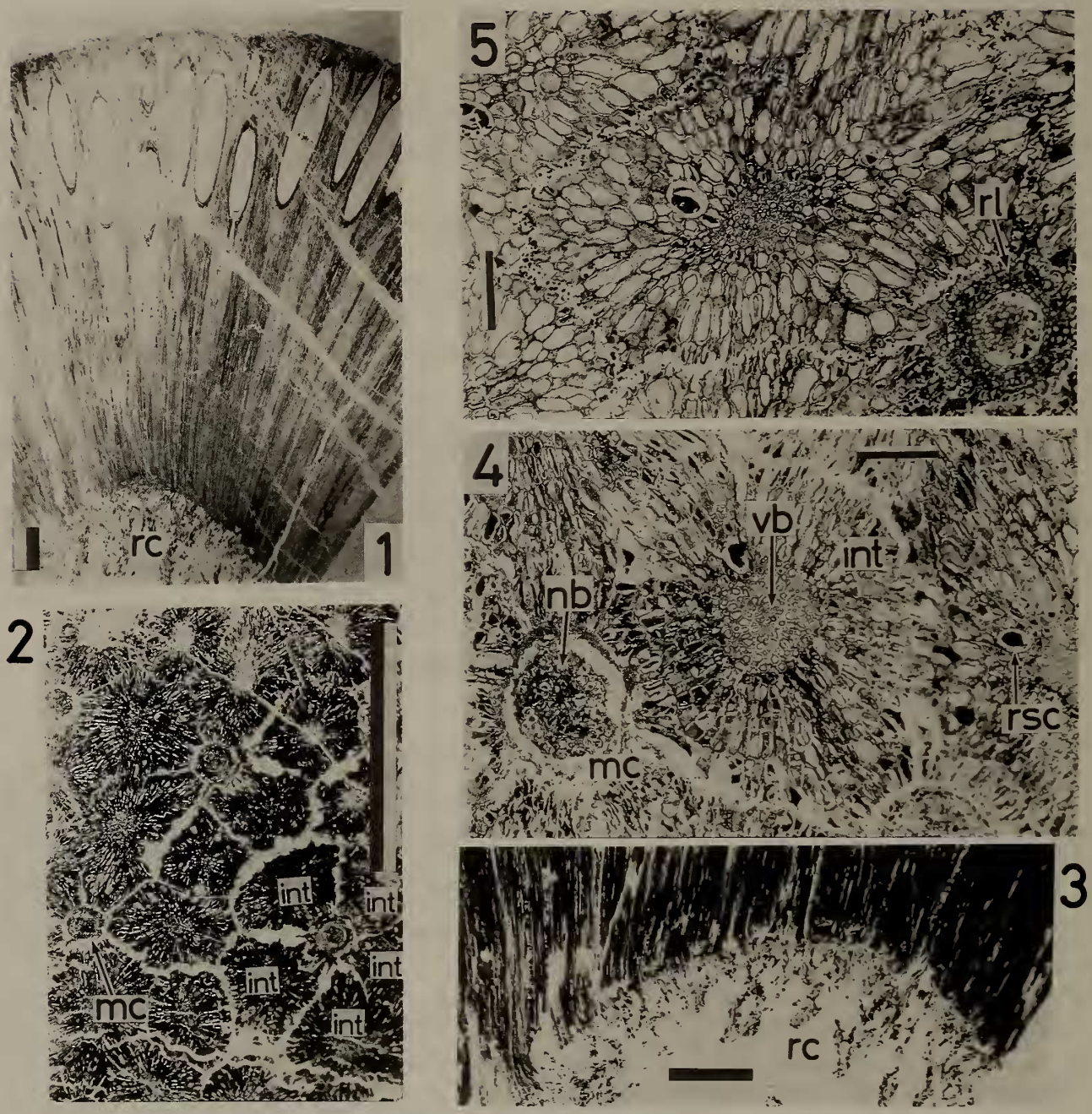

Figure 2. *Bennetticarpus yezoites* sp. nov. All sections were made from INH-005. Thick and thin scale-bars indicate 2 mm and 200 μm respectively. **1**: Radial longitudinal section of a gynoecium with partly preserved hemispherical receptacle (rc; 15 mm in diameter and 9 mm high), and closely covered seminiferous and interseminal scales (about 25 mm long). **2**: Peripheral view of seminiferous and interseminal (int) scales. A micropyle (mc; small circular tissue) is surrounded by five polygonal interseminal scale heads. Note that the presence of thickly cutinized papillae around the margins of the interseminal scale heads. **3**: Longitudinal section of receptacle (rc) and basal part of the scales. Unfortunately cellular structures of receptacle are disintegrated, and the base of the scale are unclear (at level a in Figure 1A). **4**: Transverse section slightly below the periphery (at level b in Figure 1B), showing the micropylar canals (mc) at left and right corners and interseminal scales (int). The micropylar canals are filled by nucellar beaks (nb). An interseminal scale at the center is composed of a medial vascular bundle (vb) and redially disposed parenchymatous cells. **5**: Transverse section slightly below the former section (at level c in Figure 1B), showing the micropylar canal surrounded by thick walled radial cells layer (rl). Large resinous cells with dark contents (rsc) are scattered in the interseminal scales.

layer. Micropylar canal longer and circular in cross section, surrounded by five interseminal scales. Seminiferous scale having an inner layer of darkish, elongate cells, a middle layer of radial cells, and an outer layer of tubular cells. Tubular cell layer being thick below the chalazal region, otherwise thin. Radial cell layer thickened in the region above the pollen chamber where the cross section being pentagonal.

Interseminal scales thick at the peripheral region and deformed towards the base. Cells rectangular in the apical region while tubular near the base. A thick median vascular bundle present.

Description.—The single specimen obtained is permineralized with calcium carbonate. It consists of a fragmentary seminiferous and interseminal scales and a receptacle. About one-third of the original gynoecium and receptacle is preserved as a fan-shaped form. Radius of the gynoecium including interseminal scales is about 3 cm in its transverse section and the original gynoecium is estimated to be about 9.4 cm in diameter. The receptacle (rc), is hemispherical, about 15 mm in diameter and 9 mm high, covered by numerous seminiferous (fertile) and interseminal (sterile) scales (Figure 2-1). Internal structure of the receptacle is disintegrated. We prepared numerous longitudinal and transverse peel sections from the specimen. Figures 1A and 1B are drawn on the basis of our observations of these sections. The main transversely cut planes are indicated by levels a-j (Figures 1A and 1B).

(1) Seminiferous scale (Figures 1A and 1B): The ovule (seed) is borne on a long nucellar stalk and has a micropylar canal (mc), pollen chamber (pc), archegonia? (ar), orthotropous seed space (ss), saucer-like structure (slt), chalazal region (ch) and long nucellar stalk (ns) with a vascular bundle (vb). Unfortunately details of basal disintegrated parts (level a in Figure 1A) of the scales are indistinct.

These tissues are surrounded by a layer of parenchymatous tubular cells (ptc) outside, robust radial layer (rl), and a layer of dark elongate cells (dec) inside. Remains of the nucellar tissue (nt) are present along the outer margin of seed space (ss).

In addition, structureless fleshy layers (fl) are present below the micropylar canal and below the saucer-like tissue.

1) Micropylar canal (Figures 2-2, 4, 3-3): This canal is slightly projected out of the general surface of the interseminal scale heads, and is circular in transverse section, 320 μm in diameter. The canal is 900 μm long, and is filled by longitudinally elongated parenchymatous cells, forming a nucellar beak (or plug) (nb).

2) Pollen chamber (Figure 3-1) is present below the nucellar beak, but pollen grains were not observed. Archegonium-like tissue (ar) is seen below the pollen chamber.

3) Seed space (Figure 5-1) is elongately elliptical, 7.25 mm long and up to 1.85 mm wide, circular or oblong in transverse section (Figure 5-2). No structure is seen inside the seed space except for the remains of the nucellar tissue (nt).

4) Nucellar stalk (ns): This stalk develops from the base of the seminiferous scale, 14.5 mm long and 0.5 mm wide (Figure 1A), running to the base of the saucer-like tissue (slt). The vascular bundle in the nucellar stalk (ns) consists of scalariform tracheids (Figures 4-2, 4, 5-3, 4). The bundle diverges into the saucer-like tissue as fibrous strands. These fibrous strands join the thin remains of nucellar tissue, 2-3 cells thick, located along the outer wall of the seed space (Figure 4-1, 4).

The saucer-like tissue consists of nearly isodiametric small cells each with scalariform ornamentation on the cell walls (Figure 4-2, 3).

5) Radial layer (rl): The cells of the radial layer are thick-walled and cube-like. This layer originates from the part of the micropylar canal as a single row, laterally expanding at the shoulder area in two rows, running downward as a single row, and then thinning out at the upper part of the nucellar stalk. Longitudinally, this looks like a brick-shaped layer.

The thickest part of the radial layer, cut at the shoulder region, shows a pentagonal outline in transverse section and is constructed by two radial rows of cells (level d in Figure 1B). Cellular details just around the pentagonal tissue are indistinct (Figure 3-2, 3).

6) Layer of dark elongate cells (dec): This layer originates from the part of the micropylar canal, running downward along the outer margin of the seed space, broadening at the chalazal region and upper part of the nucellar stalk, then thinning out (Figure 4-1, 4).

7) Layer of tubular cells: This parenchymatous layer (ptc) is the outermost coat of the seminiferous scale. It originates from the micropylar region running downward as a very thin coat.

Thickness of this layer increases from the lower part of the seed space to the nucellar stalk region. Consequently the basal half of the seminiferous scale (below level j in Figure 1B) is occupied by nucellar stalk (ns) surrounded by a layer of thick parenchymatous tubular cells.

The tubular cells, as shown in Figures 4-1, 5-5, 6 (ptc), are elongate in longitudinal section, typically 1056 μm long, fusiform, pointed at both ends. Their walls are thin and smooth, and septum (or end wall) is not present. In transverse section [Figure 6-1—6 (ptc)], the tubular cells appear circular or oval, 55 μm in diameter. They are loosely arranged with many scattered intercellular spaces.

8) Integument: It is difficult to identify integument in the present seminiferous scales. However, the layers of tubular cells, radial cells and dark elongate cells might belong to the integument. It is noted that the above three layers do not receive any vascular supply.

9) Nucellar stalk: The lower half of the seminiferous scale consists of concentrically arranged cell layers. At the level f of the transverse section as shown in Figure 6-1, the layer of tubular cells is the outermost, followed, from outside to inside, by radial (rl), dark elongate (dec), fleshy (fl), saucer-like tissue (slt) and the base of seed space. The fleshy layer is an empty space (Figures 1B, 3-1, 4-1, 4).

The center of the nucellar stalk is almost without structure, and in transverse section the vascular bundle is located centrally (Figure 5-4) or often laterally, and is pinned against the margin of a fleshy circular cylinder (Figures 5-3, 6-3, 4, 5, 6).

Surrounding cells in transverse section are normally oval-shaped (Figure 6-4).


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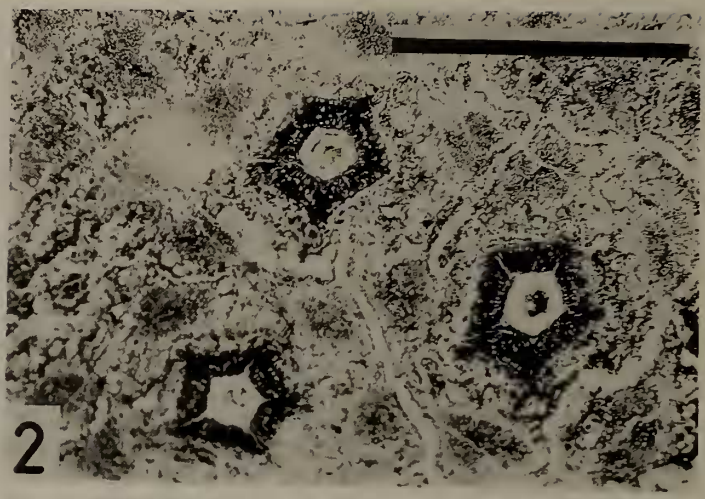
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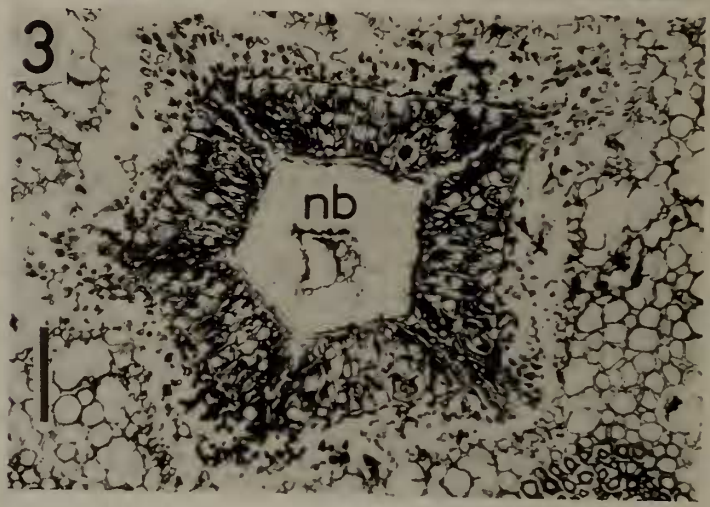
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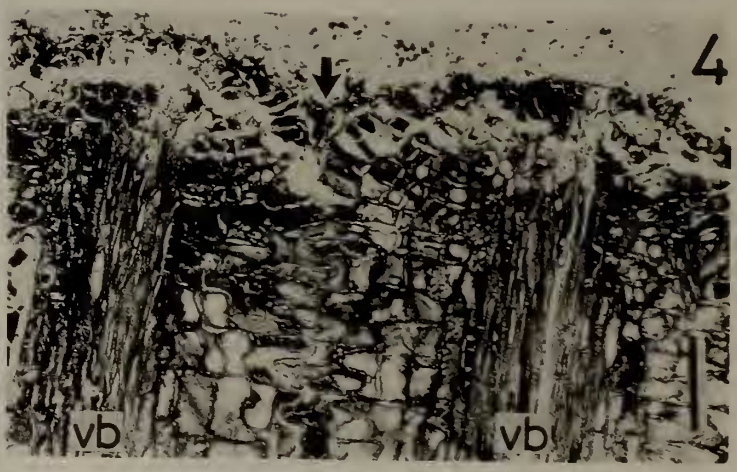
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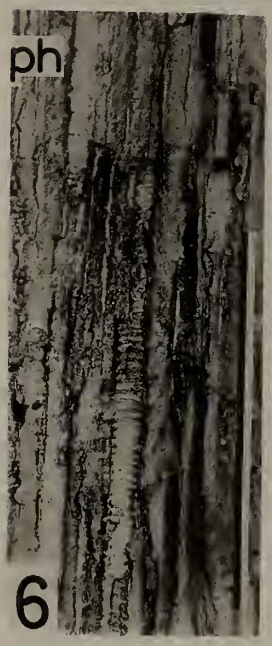
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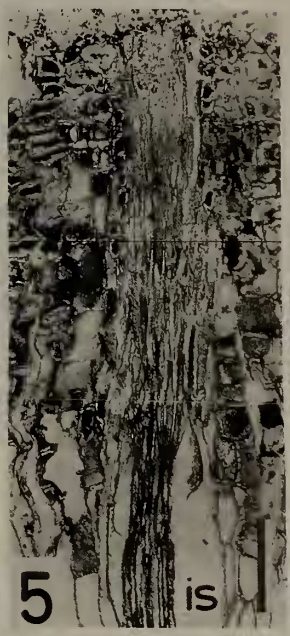
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(2) Interseminal scale : This scale is sterile, club-shaped, and its distal part is expanded transversely with a median vascular bundle throughout. In surface view, interseminal scale heads are polygonal, and five scale heads surround the small circular micropyle.

The heads are dark due to the heavily cutinized and thick-walled cells which are radially elongated. Thickly cutinized papillae are present on the margins of the interseminal scale heads (Figure 2-2).

Under the peripheral surface (at level b in Figure 1B), most cells are light-colored, because of the absence of thick-walled and heavily cutinized cells. The center of the interseminal scale is occupied by a thick median vascular bundle (Figure 2-4, 5). Large-sized resin cells with dark contents are present. In the longitudinal section, thick epidermal and hypodermal cell layers are present (Figure 3-4). Under the hypodermis, cells are cubic or rectangular and stacked like bricks (Figure 3-4). Vascular bundle consists of tracheids with scalariform thickening (Figure 3-5, 6).

The lower half of the interseminal scale is markedly deformed and its cells are small-sized, parenchymatous and loosely arranged. These cells correspond to the tubular cells of the seminiferous scales. Layer of these small-sized cells surrounds the tubular cell layer of the seminiferous scale (Figure 6-6, 7, 8). Large-sized resin cells with dark contents are also present. Such resin cells are not found in the seminiferous scale.

The so-called 'boss', arising on the center of an interseminal scale head (Harris, 1932) is not observed, and so also stomata said to be located around the boss are not observed in our interseminal scale head. Our scale heads are slightly convex as seen in the longitudinal section (Figure 3-4).

Discussion and comparison

The specimen described here is a fragment of a permineralized gynoecium, consisting of a receptacle bearing numerous interseminal and seminiferous scales. Except for the receptacle, the fossil is well preserved, allowing the preparation of numerous serial peel sections along longitudinal and transverse surfaces. Figure 1A shows the entire structure of seminiferous and interseminal scales and Figure 1B shows the enlarged upper half of the scales mainly on the basis of longitudinally cut section.

The terminology for the tissues in bennettitalean gynoecium varies according to the authors, except for the micropylar canal, nucellar beak and pollen chamber, because the function of other tissues is still uncertain.

The present structure is characterized by its rather large-sized scales (24 mm long and up to 1.5 mm in diameter) similar to those of *Cycadeoidea morierei* (Saporta and Marion) Seward (30-45 mm long and up to 1.5 mm in diameter) (e.g. Seward, 1917). Another characteristic feature of the present gynoecium described here is the presence of a thick radial cell layer at the shoulder region above the seed space (Figure 3-1, 2, 3), similar to those recorded for *Cycadeoidea dartoni* Wieland (Wieland, 1916, fig. 46), *C. dacotensis* (MacBride) Ward (Wieland, 1916, fig. 47), *C. morierei* (Saporta and Marion) Seward (in Seward, 1917) and *C. wielandi* Ward (Wieland, 1906, fig. 63-1).

This tissue was called prismatic layer for *Cycadeoidea morierei* (Wieland, 1906), radial and tubular layers (Seward, 1917), and a slightly palisaded layer of heavily walled cells for *C. wielandi* (Wieland, 1906). A thick radial layer appears to be restricted to some *Cycadeoidea* species and has not yet been found in *Williamsonia* species and its allies.

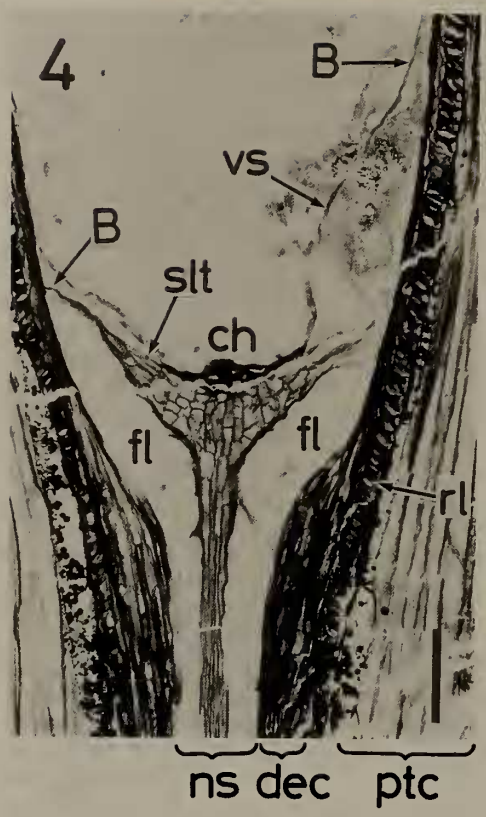
However, as said earlier regarding terminology of tissues, in *Cycadeoidea morierei,* the parenchymatous tubular cell layer is called tubular envelope (Wieland, 1906 ; Seward, 1917) and in *C. wielandi*, this layer is said to be the continuation of the heavy-walled tubular cells (Wieland, 1906).

According to Stewart and Rothwell (1993), the integument of *Cycadeoidea morierei* corresponds to the fibrous layer, an extension of the nucellar stalk. This layer may correspond to our layer of dark elongate cells. However, we believe that the radial layer is real integument, because it envelopes the internal tissues throughout.

Sharma (1977, 1990) made some ontogenic studies on the *Williamsonia* ovules and mentioned that ovule development was basipetal. But in our gynoecium, such a trend is not observed. The developmental stage of our gynoecium is still uncertain.

Nishida (1994) redescribed *Cycadeoidella japonica* Ogura from the Turonian Middle Yezo Group, Hokkaido. In this species the vascular bundle does not enter the outer margin of nucellar remains. In his interseminal scale head, cells appear to be not radially arranged and nearly isodiametric. These features are different from those of our interseminal

Figure 3. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μm respectively. **1**: Radial longitudinal section of an upper part of the ovule, composed of micropylar canal filled by nucellar beak (nb), pollen chamber (pc), archegonium ? (ar), and outer radial layer (rl) in two rows at the shoulder region. Along the micropylar region, swollen interseminal scales are close to the micropylar canal. Thin structureless fleshy layer (fl) is present inside the radial layer. **2**: At the shoulder region cut at level d (Figure 1B), pentagonal radial layers are present, composed of two rows of thick walled cells radially arranged. Each angle is separated by narrow wing-like tissue. In other part, the radial layer is a single row. **3**: Pentagonal radial layer enlarged from Figure 3-2. Broken nucellar beak (nb) is seen. **4**: Radial longitudinal section of distal part of two interseminal scales. An arrow shows the position of boundary between two scales. Each scale is penetrated by a rather thick median vascular bundle (vb). The scale head is slightly convex and is composed of heavily cutinized epidermal and thick-walled hypodermal cell layers. The ground tissue is composed of rectangular cells and looks like a stack of bricks. **5**: Vascular bundle in longitudinal section of an interseminal scale, and the presence of intercellular spaces (is). **6**: Longitudinal section of scalariform tracheids at the proximal portion of an interseminal scale. Note that the surrounding cells are longitudinally elongated, instead of rectangular cells at the apical portion of scale. Some elongate cells are thought to be phloem elements (ph).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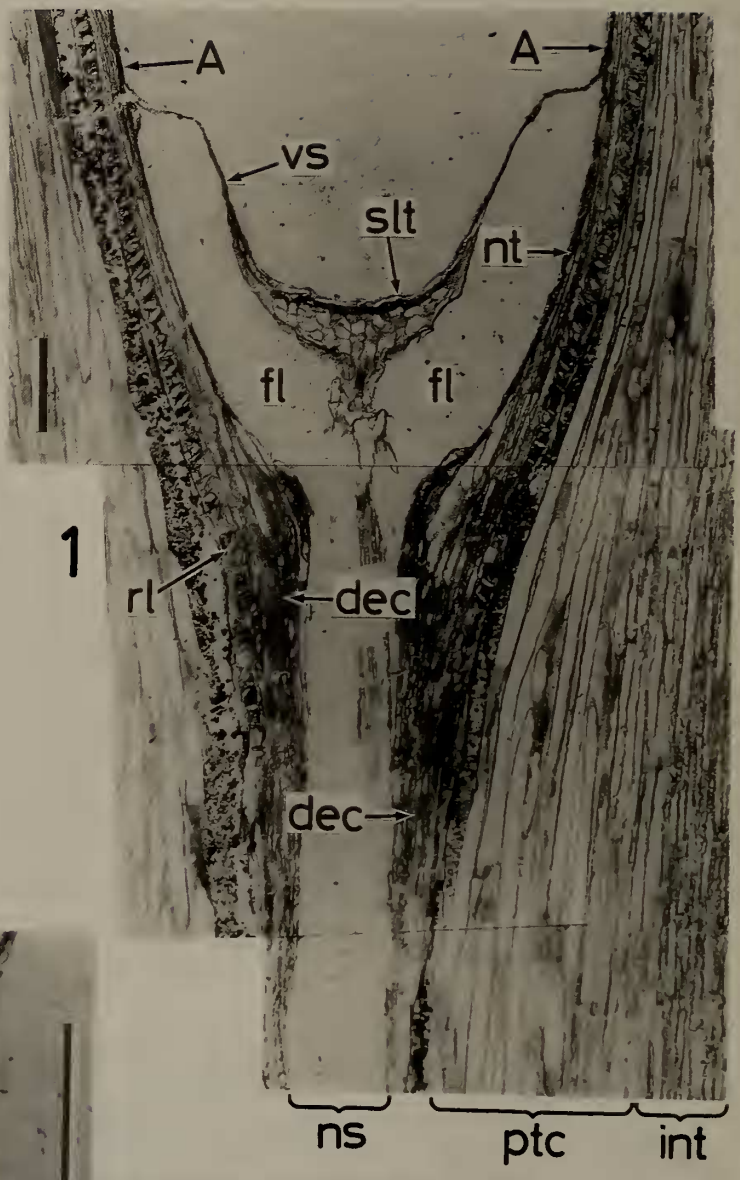
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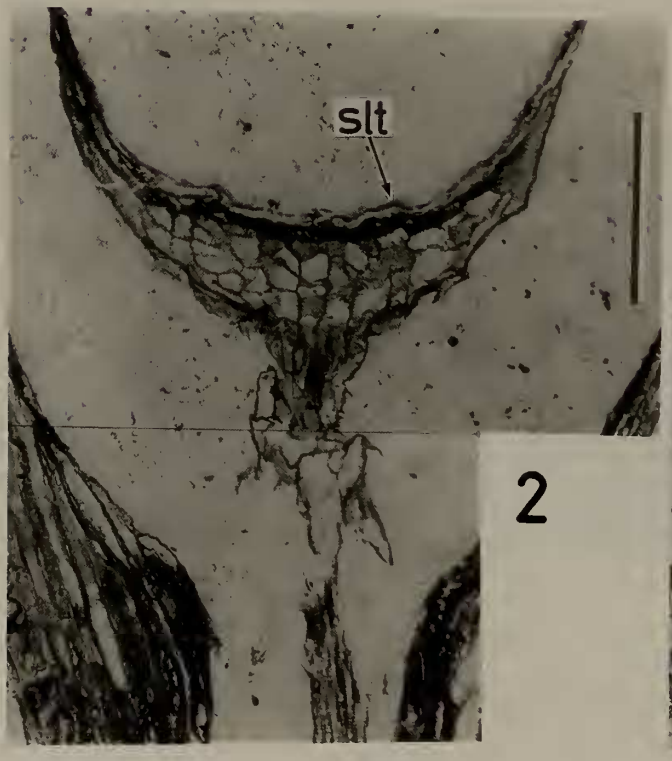
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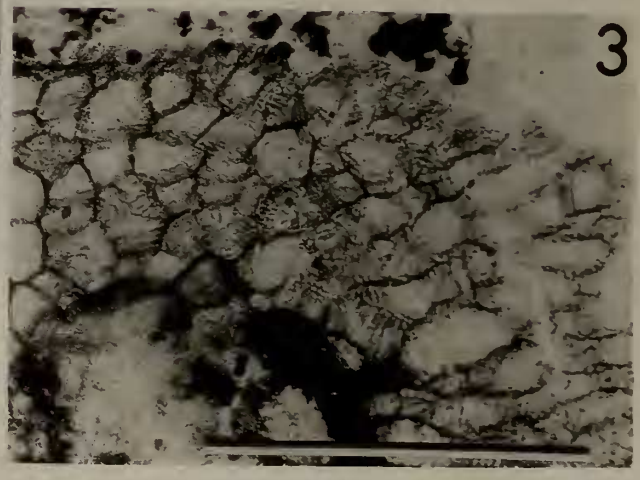
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scales. Further, he showed outer structureless membranes which respectively did envelope the seminiferous and the interseminal scales throughout. However, such a membraneous structure is not observed in our gynoecium.

The structure of the bennettitalean scales at the base has been illustrated in various ways as, for example, in *Williamsonia* sp. (Sharma, 1970, 1974), *W. sewardiana* Sahni (Sahni, 1932), *W. scotica* Seward (Seward, 1912) and *Cycadeoidea* sp. (Crepet, 1974). Unfortunately, the basal details of our scales are not clear (Figure 2-1, 3).

At present, it is difficult to establish the generic affinity of our gynoecium, which is represented only by a receptacle and a thick layer of seminiferous and interseminal scales.

Nevertheless, it is clear that the present gynoecium is bennettitalean. Numerous permineralized bennettitalean reproductive organs have been recorded from Mesozoic plant sites, but the internal features of their gynoecia are different from the present specimen. Under the circumstances we assign the specimen to the bennettitalean form-genus *Bennetticarpus* with the specific name *Bennetticarpus yezoites* untill additional information is available.

Acknowledgments

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References cited

Crepet, W.L., 1974: Investigations of North American cycadeoids: The reproductive biology of *Cycadeoidea*. *Palaeontographica*, Abt. B, Bd. 148, p. 144-169, pls. 52-72.

Harris, T.M., 1932: The fossil flora of Scoresby Sound East Greenland. Part 3: Caytoniales and Bennettitales. *Meddelelser om Grønland*, Bd. 85, no. 5, p. 1-133, pls 1-19.

Harris, T.M., 1969: *The Yorkshire Jurassic flora* III. vi+186 p. pls. 1-7. British Museum (Natural History).

Hsü, J., 1948: On some fragments of bennettitalean 'flowers' from the Liling Coal Series of East Hunan. *In* 15th Aniversary Paper of the Peking University, Series Geology, p. 57-68, pls. 1-2.

Kräusel, R., 1949: Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Österreich. *Palaeontographica*, Abt. B, Bd. 87, p. 35-82, pls. 6-18.

Nishida, H., 1991: Diversity and significance of Late Cretaceous permineralized plant remains from Hokkaido, Japan. *Botanical Magazine*, Tokyo, vol. 104, p. 253-273.

Nishida, H., 1994: Morphology and the evolution of Cycadeoidales. *Journal of Plant Research*, vol. 107, p. 479-492.

Nishida, H., Nishida, M. and Ohsawa, T., 1991: Use of fluorescent microscopy in defining a small ligule-like ovuliferous scale of a permineralized taxodiaceous cone from the Upper Cretaceous of Hokkaido, Japan. *Botanical Magazine*, Tokyo, vol. 104, p. 231-234.

Nishida, M., Nishida, H. and Ohsawa, T., 1991: *Yezosequoia shimanukii* gen. et sp. nov., a petrified taxodiaceous cone from Hokkaido. *Journal of Japanese Botany*, vol. 66, no. 5, p. 280-291.

Nishida, M., Ohsawa, T. and Nishida, H., 1992: *Parataiwania nihongii* gen. et sp. nov., a taxodiaceous cone from the Upper Cretaceous of Hokkaido. *Journal of Japanese Botany*, vol. 67, no. 1, p. 1-9.

Ogura, Y., 1930: On the structure and affinities of some Cretaceous plants from Hokkaido. *Journal of Faculty of Science, Tokyo Imperial University*, sec. 3, vol. 2, pt. 5, p. 381-412, pls. 18-21.

Ohana, T. and Kimura, T., 1991: Permineralized *Otozamites* leaves (Bennettitales) from the Upper Cretaceous of Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, n.s., no. 164, p. 944-963.

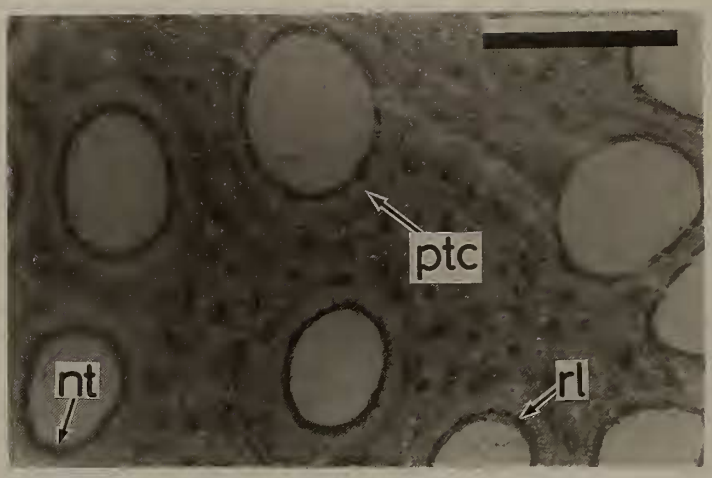
Ohana, T. and Kimura, T., 1993: Permineralized *Brachyphyllum* leafy branches from the Upper Yezo Group (Coniacian-Santonian), Hokkaido, Japan. *Bulletin of the National Science Museum,* Tokyo, ser. C, vol. 19, no. 2, p. 41-64.

Ohana, T. and Kimura, T., 1995: Further observations of *Cunninghamiostrobus yubariensis* Stopes and Fujii from the Upper Yezo Group (Upper Cretaceous), Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, n.s., no. 178, p. 122-141.

Ohsawa, T., Nishida, H. and Nishida, M., 1991: A petrified pinaceous cone from the Upper Cretaceous of Hokkaido. *Journal of Japanese Botany*, vol. 66, no. 6, p. 356-368.

Ohsawa, T., Nishida, H. and Nishida, M., 1992: A cupressoid seed cone from the Upper Cretaceous of Hokkaido.

Figure 4. *Bennetticarpus yezoites* sp. nov. Thin scale-bar indicates 200 μm. **1**: Radial longitudinal section of the middle portion of a seminiferous scale. Nucellar stalk (ns) is slender consisting of scalariform tracheids, running upward and diverging in the saucer-like tissue (slt) as fibrous vascular strands (vs). This strand merges into the thin layer of nucellus remains at the outer marginal part of the seed space (Arrow A). Dark elongate cell layer (dec) is thickest just above the level h in Figure 1B, thinning out upward and downward. At level f (Figure 1B), this layer merges into the remains of nucellus (nt). Outside the radial layer (rl), this layer is enveloped by long and thin walled tubular cell layers (ptc), and is in contact with more narrow tubular cell layers of neighboring interseminal scales (int). Note that this figure was made by adjoining two photographs, consequently there is a small offset where they meet. **2**: Saucer-like tissue (slt) enlarged from Figure 4-1. **3**: Transverse section of the saucer-like tissue (at g-level in Figure 1B). Cells are nearly isodiametric and their cell walls are ornamented by scalariform pattern. **4**: Radial longitudinal section of the nucellar stalk. The fibrous vascular strand (vs) is about to enter and merge into the remains of the nucellus (Arrow B). Structureless fleshy layer (fl) is seen around the nucellar stalk and saucer-like tissue.



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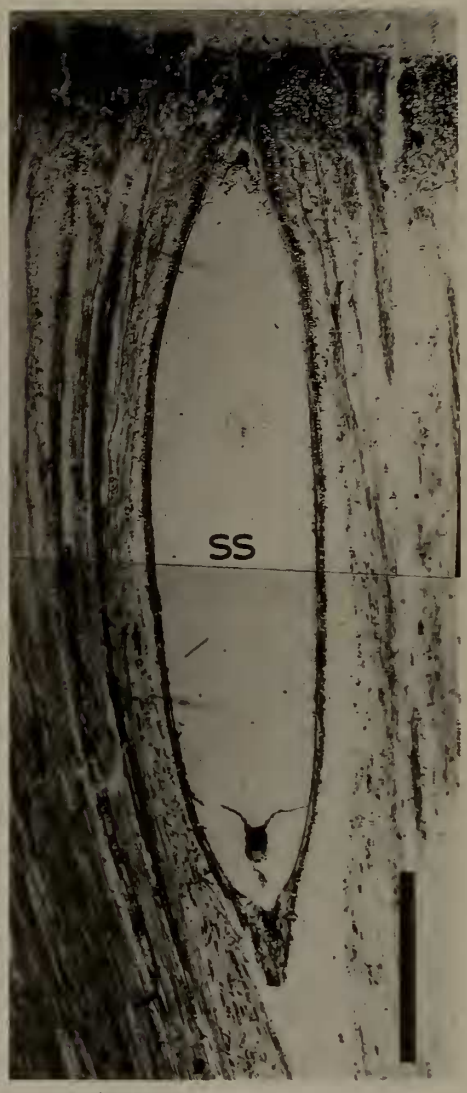

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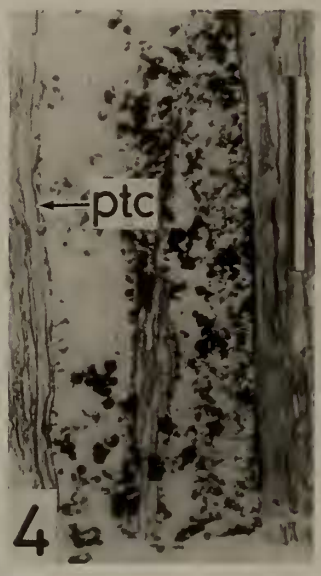

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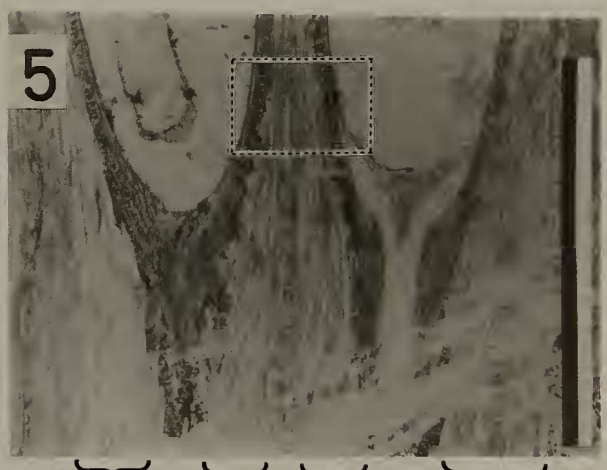

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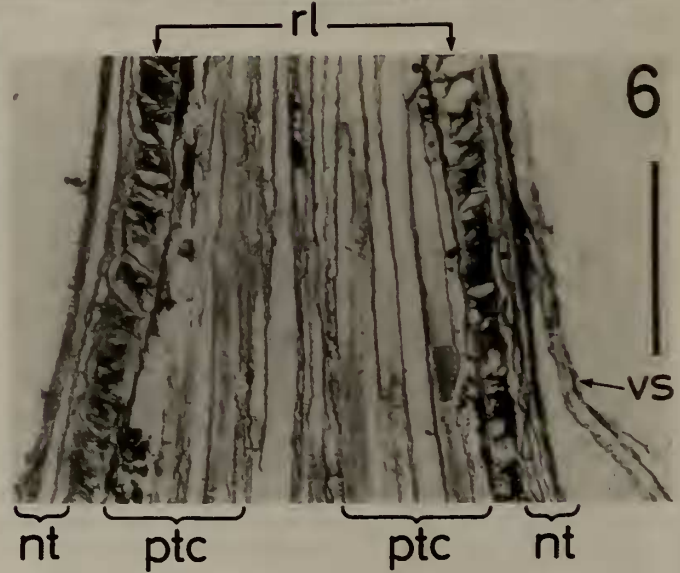

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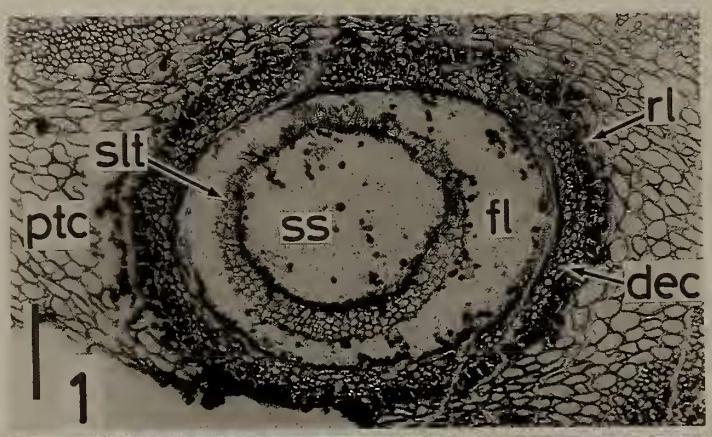
Botanical Magazine, Tokyo, vol. 105, p. 125-133.
Ohsawa, T., Nishida, H. and Nishida, M., 1993 : *Yubaristrobus* gen. nov., a new taxodiaceous cone from the Upper Cretaceous of Hokkaido. *Journal of the Plant Research*, vol. 106, p. 1-9.
Ohsawa, T., Nishida, M. and Nishida, H., 1992 : Two *Sequoia*-like cones from the Upper Cretaceous of Hokkaido. *Journal of Japanese Botany*, vol. 67, no. 2, p. 72-82.
Sahni, B., 1932 : A petrified *Williamsonia* (*W. sewardiana* sp. nov.) from the Rajmahal Hills, India. *Palaeontologica Indica* (New Series), vol. 20, no. 3, p. 1-19, pls. 1-3.
Saiki, K., 1992 : A new sciadopityaceous seed cone from the Upper Cretaceous of Hokkaido, Japan. *American Journal of Botany*, vol. 79, no. 9, p. 989-995.
Saiki, K. and Kimura, T., 1993 : Permineralized taxodiaceous seed cones from the Upper Cretaceous of Hokkaido, Japan. *Review of Palaeobotany and Palynology,* vol. 76, p. 83-96.
Seward, A.C., 1912 : A petrified *Williamsonia* from Scotland. *Philosophical Transactions of the Royal Society*, ser. B, vol. 203, p. 101-126, pls. 9-12.
Seward, A.C., 1917 : *Fossil plants. A text-book for students of botany and geology*. vol. 3. xviii+656 p. Cambridge.
Sharma, B.D., 1970 : On the structure of the seeds of *Williamsonia* collected from the Middle Jurassic rocks of Amarjola in the Rajmahal Hills, India. *Annals of Botany*, vol. 34, p. 1071-1078, pl. 1.
Sharma, B.D., 1974 : Ovule ontogeny in *Williamsonia* Carr. *Palaeontographica*, Abt. B, Bd. 148, p. 137-143, pls. 49-51.
Sharma, B.D., 1977 : Indian *Williamsonia*- An illustrated review. *Acta Palaeobotanica*, vol. 18, no. 1, p. 19-29.
Sharma, B.D., 1990 : Morphology of bennettitalean fructifications. *Palaeobotanist*, vol. 38, p. 163-170.
Stewart, W.N. and Rothwell, G.W., 1993 : *Paleobotany and the evolution of plants*. xii+521 p. Cambridge University Press.
Stockey, R.A., Nishida, H. and Nishida, M., 1993 : Upper Cretaceous araucarian cones from Hokkaido ; *Araucaria nihongii* sp. nov. *Review of Palaeobotany and Palynology*, vol. 72, p. 27-40.
Stockey, R.A., Nishida, H. and Nishida, M., 1994 : Upper Cretaceous araucarian cones from Hokkaido and Saghalien ; *Araucaria nipponensis* sp. nov. *International Journal of Plant Sciences*, vol. 155, no. 6, p. 806-815.
Stopes, M.C. and Fujii, K., 1910 : Studies on the structure and affinities of Cretaceous plants. *Philosophical Transactions of the Royal Society*, ser. B, vol. 201, p. 1-90, pls. 1-9.
Watson, J. and Sincock, C.A., 1992 : *Bennettitales of the English Wealden*. Monograph of the Palaeontological Society. 228 p., 23 pls.
Wieland, G.R., 1906 : American fossil cycads. Carnegie Institution of Washington, Publication, no. 34. viii+296p., pls. 1-50.
Wieland, G.R., 1916 : American fossil cycads. vol. II. Taxonomy. Carnegie Institution of Washington, Publication, no. 34. vii+277 p., 58pls.

Figure 5. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μm respectively. **1** : Nearly radial longitudinal section of an orthotropous ovule. Neighboring interseminal scales are curved as a result of the corpulence of the seed space. Peripheral layers are darkish because of thick-walled and heavily cutinized cells. **2** : Transverse section of seed spaces. Each space is surrounded, from inside to outside, by remains of nucellus (nt), dark elongate cells, radial and parenchymatous tubular cell layers, cut at level e (Figure 1B). Both dark elongate cells and radial cell layers are darkish. Among these seed spaces many interseminal scales are seen. Dark dots show the transverse section of the vascular bundles. **3** : Longitudinal section of scalariform tracheids in nucellar stalk. They are often pinned against the wall of fleshy cylinder (cf. Figure 6-5, 6). **4** : Longitudinal section of poorly preserved tracheids in the nucellar stalk. **5** : Longitudinal section of two ovules. Both nucellar stalks are surrounded by radial layers inside and parenchymatous tubular cell layers (ptc) outside. **6** : Enlarged from the boxed area in Figure 5-5. A fibrous vascular strand (vs) enters into and merges with remains of the nucellar tissue (nt).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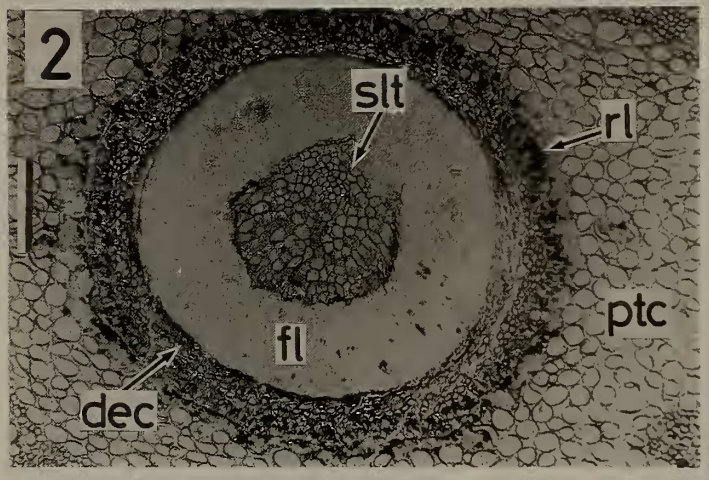
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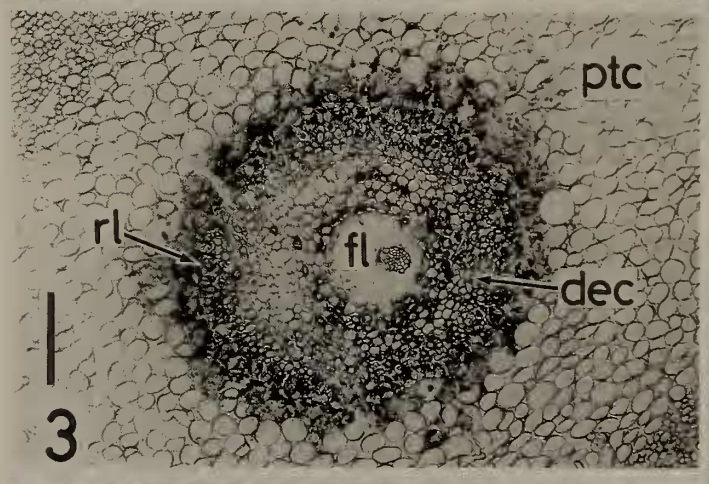
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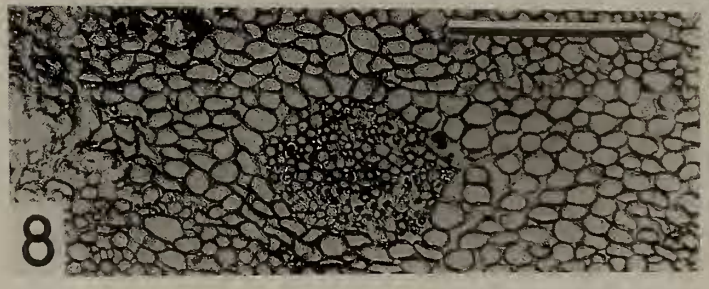
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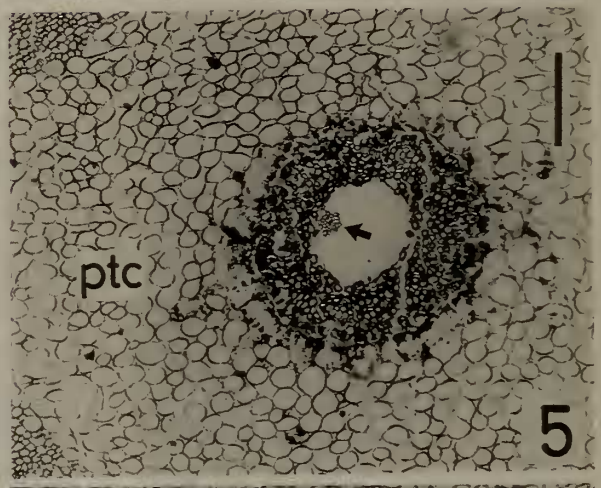
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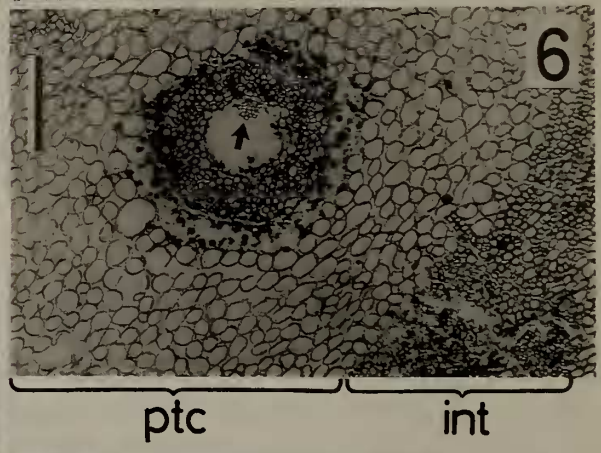
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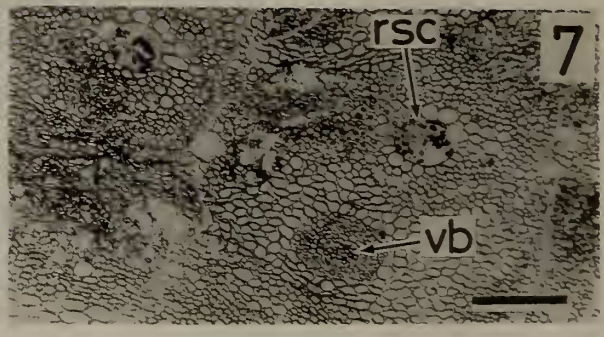
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Figure 6. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μm respectively. **1**: Transverse section cut at level f (Figure 1B). Concentric tissues, from outside to inside, are: darkish radial layer (one cell thick and single row) (rl), layer of dark elongate cells (dec), structureless fleshy layer (fl), saucer-like tissue (slt) and bottom of the seed space (ss). These tissues (or layers) are enveloped by parenchymatous tubular cells layer (ptc). Layers of small cells seen at three corners belong to the neighboring interseminal scales. **2**: Transverse section cut at level g (Figure 1B). Concentric tissues, from outside to inside, are: radial layer (one cell thick) (rl), layer of dark elongate cells (dec), structureless fleshy layer (fl) and saucer-like tissue (slt). They are enveloped by a layer of parenchymatous tubular cells (ptc). **3**: Transverse section cut at level h (Figure 1B). Three concentric tissues are seen; they are in turn, radial layer (one cell thick) (rl), dark elongate cells layer (dec) and structureless fleshy layer (fl). Vascular bundle is seen in the fleshy cylinder. **4**: Transverse section cut at level i (Figure 1B). Darkish ring consists of thin radial layer and dark elongate cells layer. Parenchymatous tubular cells layer (ptc) is usually oval-shaped. **5**: One-sided location of the vascular bundle (arrow) in the fleshy cylinder. **6**: The same. Small-sized cells belong to the neighboring interseminal scales (int). **7**: Transverse section of deformed interseminal scales cut at level j (Figure 1B), showing vascular bundle (vb) and many scattered resin cells (rsc). **8**: A vascular bundle enlarged from Figure 6-7. It is difficult to distinguish the phloem elements.